

Call me invasive: Testing the first impacts of the alien mantises *Hierodula patellifera* and *Hierodula tenuidentata* on European biodiversity

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Abstract

The Asian mantises *Hierodula tenuidentata* and *Hierodula patellifera* are known alien species rapidly spreading in the last few years in the Mediterranean and continental Europe, especially in urban and suburban habitats, although their invasive nature is debated. This study investigated the first set of impacts of these species on European ecosystems, measuring the prolificacy and reproductive potential with inferences on native mantises, the presence of positive and negative interactions with other species—both as prey and predators—and other peculiar behaviors leading to possible ecosystemic impacts. Laboratory data has shown high reproductive output, with *H. tenuidentata* hatching on average 209 nymphs per ootheca, about twice that of the native *Mantis religiosa*, and low cannibalism rates during first instars, supporting rapid and competitive population growth. Behavioral tests revealed reproductive interference: *M. religiosa* males are attracted to *Hierodula* females and are therefore preyed upon, a “fatal attraction” that may reduce mating success in native species. A large set of citizen science reports (over 2,300 records) document *Hierodula* predation on a wide range of native species, from pollinators to small vertebrates often protected by EU legislation, such as *Podarcis muralis* and *Hyla perrini*. *Hierodula* mantises show trophic generalism, preying on a wide range of insect taxa and occasionally competing with native mantises or even hornets, revealed to be their main natural predators. Their use of human-modified environments and artificial refuges highlights their adaptability. The different impacts recorded and measured here are discussed within the IUCN criteria for invasive species, confirming the *Hierodula* in Europe as invasive alien species.

Keywords

Biocontrol, cannibalism, competition, *Hierodula*, IAS, invasive alien species, predation

Introduction

Different species of mantises have recently been recorded outside their native range and classified as alien species. This is known to occur since at least the XIX century in the Nearctic area (Gurney 1951, Anderson 2018), where the pace of introductions has greatly

increased over the past few decades (Shcherbakov and Govorov 2020), to more recently in Hawaii (Howarth and Mull 1992) and New Zealand (Ramsay 1984), while the first alien species arrived later in the Palearctic region in Portugal (Marabuto 2014), and Europe has since been widely colonized by at least two species of the Asian mantis genus *Hierodula* Burmeister, 1838. Other species are under monitoring in the Eurasian area (Schwarz and Ehrmann 2018, Shcherbakov and Govorov 2020). Of particular relevance is the case of Asian mantises, with the species *Hierodula tenuidentata* Saussure, 1869, naturally distributed from Central and South Asia to East Europe and *Hierodula patellifera* Serville, 1839, naturally distributed in far East Asia and Indonesia, both recently introduced in southern Europe and now having large, stable, and spreading populations, especially in the southern Balkans and in northern Italy, but with a large number of single or multiple local observations across most of the European countries (Ehrmann 2011, Ehrmann and Borer 2015, Pushkar and Kavurka 2016a, b, Battiston et al. 2018, Schwarz and Ehrmann 2018, Romanowski et al. 2019, Battiston et al. 2020a, Battiston et al. 2020b, Pintilioaie et al. 2021, van der Heyden 2018, 2021, Vujić et al. 2021).

In general, the impacts of alien mantises on native species or ecosystems are not completely understood, and studies on them are extremely scarce and typically related to particular situations or species (Fea et al. 2013). Mantises are mostly generalist and often voracious predators, and they unquestionably have multi-level impacts on local communities by reducing the numbers of their prey or competing with other species (Prete et al. 1999). Moreover, the species studied in New Zealand (Fea et al. 2013) and some anecdotal observations in Italy, mostly from citizen science (i.e., Fig. 1), suggest that pheromone attraction is often weakly species-specific in many mantis species and may lead to interspecific predation, which can strongly affect native species populations. *Mantis religiosa* (Linnaeus, 1758) is a species widely distributed in Eurasia and Africa and introduced in North America (<https://www.gbif.org/species/4394789>) and, in some native regions, its distribution already overlaps with *Hierodula* (<https://www.gbif.org/species/4394789>).



Fig. 1. Anecdotal observations of alien mantises impacts recorded in Italy. A–C. Two males of *Mantis religiosa* attempting to mate with a female of *Hierodula tenuidentata* in a private garden, ending with the escape of one and the death of the other, eaten by the female. Photo credit: M. Mazzola. D. A voracious female of *Hierodula patellifera* Serville, 1839, feeding on two pollinators—a honey bee (*Apis mellifera* Linnaeus, 1758) and a German wasp (*Vespula germanica* (Fabricius, 1793)), the latter of which was attracted by the ongoing predation—sitting on a *Hedera* sp. L., 1753 inflorescence. Photo credit: R. Battiston.

[org/species/8263753](https://www.iucn.org/species/8263753)), sometimes with a long-documented coexistence (i.e., in Japan, see Giglio-Tos 1912). However, while *M. religiosa* usually lives on low vegetation such as grass or shrubs (Battiston and Fontana 2010, Battiston et al. 2020c), *Hierodula* is more tree-dwelling; thus, a possible niche separation has been suggested to moderate their interactions and the possible fatal attraction.

The extent of these interactions and impacts outside their native ranges and in forced situations, such as urban, sub-urban, or semi-natural environments where both species are expanding, is, however, practically unknown, which presents a considerable challenge for the conservation of native species and ecosystems.

Moreover, while the “alien” nature of these species is well demonstrated, their invasiveness is yet to be determined, even if these two terms are often used indiscriminately in the literature (Schwarz and Ehrmann 2018, Kawashima and Watanabe 2016, Shcherbakov and Govorov 2020, Moulin 2020). Indeed, this semantic issue prevents the application of the definition of alien invasive species (IAS) to most of these exotic mantises and represents another strong obstacle for biocontrol regulations, communication, and awareness. According to EU regulations and IUCN protocols on

IAS, the appearance of alien species in new localities is not always a cause for concern. However, if a significant subset of alien species has a serious adverse impact on biodiversity and related ecosystem services as well as on other social and economic elements, they can be considered invasive. In the EU and in other European countries, roughly 10% to 15% of alien species are considered invasive (Regulation EU 2014, IUCN 2000). Is this the case for *Hierodula*?

In this scenario, it appears a priority to evaluate the impacts of these alien mantises to understand their invasiveness and set up adequate biocontrol actions, following the proposal of preliminary guidelines for these species (Battiston et al. 2024). For this study, a laboratory pheromone attraction test was set up to evaluate the species-specific nature of sexual interaction between the most widespread alien mantises in Europe (*H. tenuidentata* and *H. patellifera*) and the native *M. religiosa*. Moreover, a large set of citizen-science observations and new original ones (Figs 4–8) were examined to allow discussion of the possible positive and negative interactions of these species with the native fauna. An evaluation of the prolificacy of *Hierodula* vs *Mantis* was also conducted to measure the potential pressure on the ecosystem during the insects’ juvenile stages.

Materials and methods

Prolificacy.—During March 2023, five undetermined oothecae of *Hierodula* sp. were collected from Castel Goffredo (MN) and ten from near Milan, both in Northern Italy but from different populations (approximately 120 km apart). They were reared separately in laboratory conditions at 20°C and moistened twice per week. All the nymphs successfully emerged one month later; they were counted, and the average number of nymphs hatched from each ootheca was used to evaluate the potential number of new predators that a single ootheca can introduce to a new environment. This number was compared with the number of nymphs hatched from native *Mantis religiosa* oothecae, according to the literature (Hideg 1991).

A total of 54 *Hierodula* nymphs from both localities were relocated to different 0.4 liter plastic boxes to evaluate intraspecific cannibalism in the early life stages. A rolled-up piece of adsorbent paper was placed inside the box to increase the surface area available for movement. A total of nine containers were set up: three containing 10 nymphs, three with 5, and three with 3. The number of individuals alive, dead, or missing (cannibalized) was checked twice a day (at dawn and dusk) for 21 consecutive days.

The purpose of the experiment was to assess the rate of cannibalism in the first weeks of life—and therefore the chance of survival in high-density artificial situations such as urban parks or restricted areas—by artificially recreating different densities of population with the absence of natural prey. As a control test, three further boxes were used: one box was randomly selected containing 10 specimens, one with 5 and one with 3, all provided with two specimens of *Drosophila melanogaster* Meigen, 1830 per nymph every two days.

Interspecific attraction.—To evaluate the species-specific chemical attraction of the males of *M. religiosa* to the signal from the females of *H. tenuidentata* and *H. patellifera*, 5 male and 5 female specimens of *M. religiosa*, 5 females of *H. tenuidentata*, and 5 females of *H. patellifera* were used. To ensure their unmated conditions, sub-adult specimens of *M. religiosa* and *H. patellifera* were collected in nature from different localities in the province of Padua (Italy). Twelve immature individuals of *H. tenuidentata* were randomly selected from the breeding and raised unmated until the adult stage to ensure at least 5 adult males and females for use in the test. They were raised under laboratory conditions following Mirzaee et al. (2022). It is extremely difficult to force reproductive behav-

ior in a serial, repeatable, and continuous manner under laboratory conditions for this type of insect, which is very sensitive to even the smallest environmental variations. Therefore, to ensure the best possible success of the attractiveness tests, a set of best practices was used to ensure that in all experiments, all females and males were in a phase of simultaneous mutual attractiveness. Tests were run between late September and late October, during the natural mating season of these species, when our individuals reached the adult stage and about two weeks had elapsed since the last molt, giving females time to begin producing pheromones (Lawrence 1992, Perez 2005). As further evidence that the pheromones emission had begun in the females, the characteristic posture of the arched pumping abdomen (Perez 2005) was observed in each female during the tests.

The specimens were placed in a special arena made of a round transparent plastic container and plastic tubes (Fig. 2) placed in a clean empty room under natural light during the daytime and soft artificial light (3 Watt LED bulb) located about 3 meters from the arena during the nighttime; this permitted a sufficient quality of video recordings and had a minimum influence on the matings by creating a diffuse-light effect. The central part of the structure (13.5 cm high, with an upper diameter of the lid of 28.5 cm and a lower diameter of 33.5 cm) had been pierced in five places. The largest of these was an upper circular hole with a diameter of 17 cm, covered by a net (cell size: 1 mm), which allowed the structure to be ventilated by directing the air flow to the center. The four other piercings held transparent straight tubes connected to the central area in opposite directions (7.5 cm diameter × 22 cm long) with a closed end where four different and unreachable sources of attraction, isolated by a barrier net, were placed. Pheromone-producing females of the two different mantis genera were placed in the ends of two diametrically opposite tubes, while the other two tubes were used as controls: one housed an individual of the cockroach *Periplaneta lateralis* (Walker 1868) to create chemical attraction of prey/food and the other was left empty.

The net at the end of each of the four tubes was placed to allow the continuous passage of air and thus of pheromones but, at the same time, prevent the male from reaching food or the females. This also minimized visual attraction by partially disrupting the shapes of the insects involved.

The purpose of this arena was to record over time the movements of *M. religiosa* males—initially placed in the central area but free to move within it—and to see which of the four sources of at-

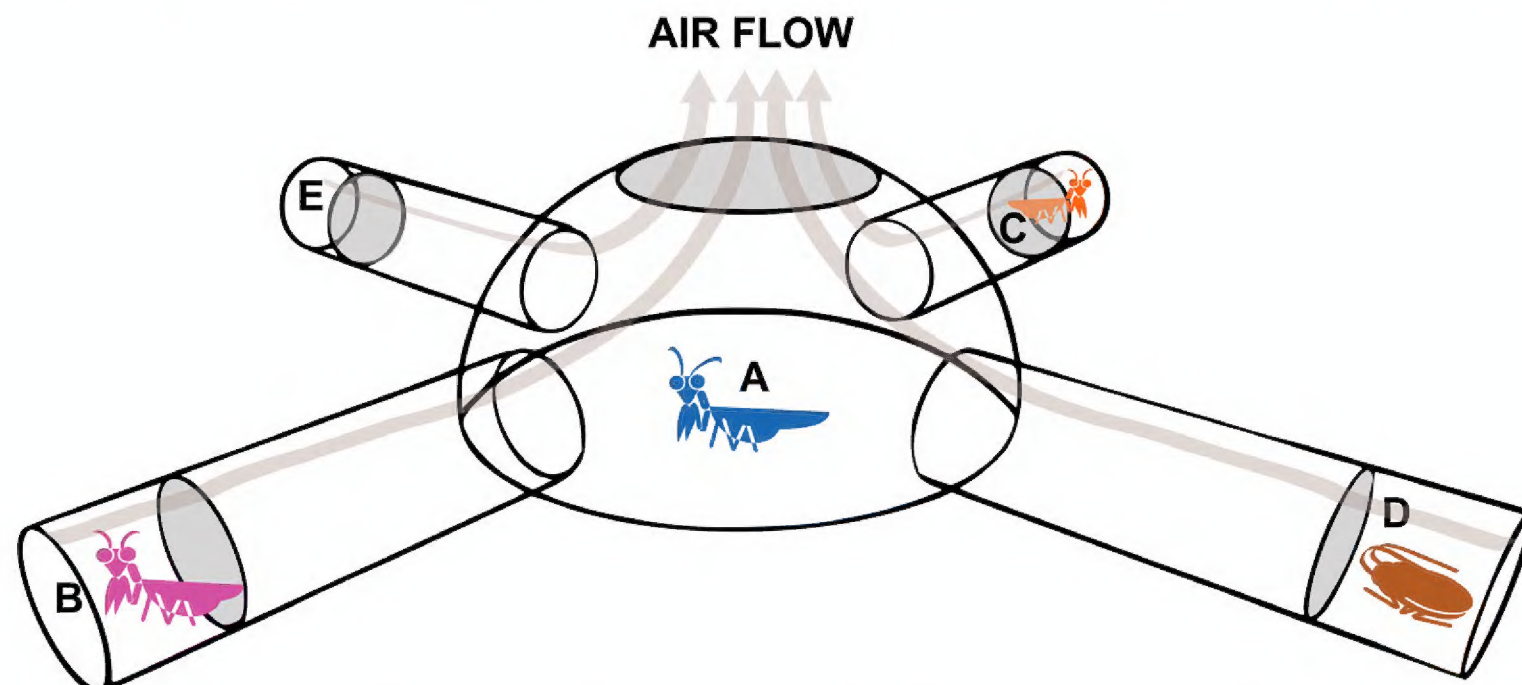


Fig. 2. Pheromone attraction test arena with A: male of *M. religiosa*, B: female of *M. religiosa*, C: female of *Hierodula* (*tenuidentata*/*patellifera*) D: food (cockroach), E: empty. Gray circles represent the net-barriers, and transparent-grey arrows represent the air-flow.

traction they would spend the most time near. Analysis of variance (ANOVA), at a significance value of 0.05, was used to evaluate the significance of the male choices comparing the number of times the male was recorded near each of the tubes.

The tests were monitored by an Oppo A16s smartphone (camera model: CPH2271), placed above the arena at a distance of 87 cm to allow the test area to be fully framed, automatically shooting a full HD image (1080×1920 at 72 dpi) every 30 seconds for 5 hours.

Each test lasted 5 hours and occurred in three different time slots, approximately from 10:00 a.m. to 3:00 p.m. (morning), 3:30 p.m. to 8:30 p.m. (afternoon), and 9:00 p.m. to 2:00 a.m. (night), to cover different daylight circles. Males and females of *M. religiosa* and females of the genus *Hierodula* were used in 50 tests, and each specimen took part in 10 of them. Each test presented a different combination of specimens: the same male or female specimens were never used in two consecutive tests, and the same triplets of specimens were taken into consideration only once to increase the randomization and significance of the outputs. To further verify the presence of environmental elements that could induce distorted behavior in males and bias the results toward sources of attraction, three tests were conducted with only the male positioned in the center of the empty arena, devoid of any sources of attraction, at the same times and under the same conditions as the other tests.

Interspecific predation.—At the end of the attraction tests, the 5 males of *M. religiosa* involved were placed, one at a time, at one end of a large mesh empty container (58×107×40 cm) for 2 hours. Two females of *H. patellifera* and three of *H. tenuidentata* were placed, one at a time, at the other end of the container. The purpose was to evaluate the presence of interspecific sexual predation between the two genera in the test condition without barriers.

Interspecific interactions.—Observed interactions between *Hierodula* and other species in Italy, including domestic and wild organisms, were collected and analyzed. A total of 2,393 reports submitted via online Google forms to the citizen science project “Progetto Mantidi Aliene” (<http://mantidialiene.netsons.org>) between June 2020 and December 2024 were processed and analyzed. Additional data from occasional posts on Italian pages of social media (e.g., Facebook, Instagram) or citizen science platforms (e.g., www.iNaturalist.org) were investigated by searching for keywords in the Italian language, such as “gatto” (cat), “mantide” (mantis), “mangiare/nutrirsi” (eating), “predazione” (preying), and “cannibalismo” (cannibalism).

Only records with clear photo/video identifiable species or at least genera and direct testimony from the reporter were considered; taxonomic identification was determined as best as possible based on the quality of the record, and then the records were sorted based on type of impact:

- Negative impacts (predation of *Hierodula* on invertebrates or vertebrates).
- Positive impacts (predation of invertebrates or vertebrates on *Hierodula* individuals or oothecae).
- Neutral impacts (cannibalism between individuals of *Hierodula*).

Interactions occurring in terrariums or other artificial/forced settings were not considered.

Results

Prolificacy.—The first nymph of the incubated oothecae hatched on April 14, 2023, and the last on the 26th of the same month. A total of 3,133 individuals hatched (avg.: 209 per ootheca), with a minimum

of 101 and a maximum of 304. A series of past experiments with *M. religiosa* found an average of approximately 127 nymphs hatched per ootheca (Hideg 1991). However, those experiments were not conducted in a controlled environment and examined a number of oothecae (227) that was larger than the sample used in this test. In the present study, the first instar nymphs of *Hierodula* showed a low rate of intraspecific cannibalism (Table 1): In the first week, only five specimens were cannibalized in one of the higher density boxes (10-nymphs container). The cannibalism rate was higher in the groups that were fed regularly, recording 9 specimens cannibalized in three weeks (total duration of the experiment), 7 in the 10-nymphs container, 1 in the 5-nymphs container, and 1 in the 3-nymphs container. Greater disturbance caused by more frequent prey movement may have influenced higher rates of predatory activity.

Interspecific attraction.—A total of 50 encounters were tested, with approximately 30,000 photos taken (an average of 600 in each test). Each photo was then examined, and the relative position of the male from the center was recorded. As expected from a sedentary predator, most time (75.5%) was spent staying still in the central part of the arena. When moving (Fig. 3), the males of *M. religiosa* were recorded in the food or in the empty tube, accounting for just 26.2% of the pictures taken, while the remaining 73.8% of the pictures were of the male heading toward the females, indicating a significantly higher propensity for sexual attraction ($F: 4.147088 > F \text{ crit.: } 3.938111$). In 39.6% of these choices, the males of *M. religiosa* opted for the female of their own species, while in 34.2%, they preferred those of the genus *Hierodula* (of this, 20.6% preferred *H. tenuidentata* and 79.4% preferred *H. patellifera*) with an insignificant difference between the two genera ($F: 0.066693 < F \text{ crit.: } 3.938111$).

During the free-ranging encounters in the mesh container, all 5 males of *M. religiosa* were captured and devoured by the 5 females of *Hierodula*. In all three control tests with the empty arena, the male remained in the central area, not attracted to any of the empty tubes, confirming the validity of the attractants, when present.

Interspecific Interactions.—A total of 86 direct interactions in 2,393 general observations were recorded: 53 (62%) negative (predation by *Hierodula*), 31 (36%) positive (predation on *Hierodula*), and 2 (2%) neutral (predation by *Hierodula* on *Hierodula*). All the interactions were recorded in urbanized environments and, in particular, on plants in private and public gardens, parks, balconies, and other domestic areas. A total of 49 negative interactions of *Hierodula* preying on insects from different orders and 4 on vertebrates were recorded: Diptera 4 (7.5%), Hymenoptera 23 (43.4%), Lepidoptera 4 (7.5%), Mantodea 5 (9.4%), Odonata 1 (2%), Orthoptera 4 (7.5%), Rhynchota 8 (15%), Amphibia 1 (2%), and Reptilia 3 (5.7%).

Nymphs of *Hierodula* exhibited a marked preference for smaller prey, such as flies: 100% of predation events recorded on Diptera were carried out by *Hierodula* nymphs (Fig. 4A), small Hymenoptera, including *Apis mellifera* Linnaeus, 1758 and *Polistes* sp. Latreille, 1802 workers, and small alien Lepidoptera (*Paysandisia archon* (Burmeister, 1880)). On occasion, they are capable of preying on larger insects, such as cicadas (*Cicada orni* Linnaeus, 1758) (Fig. 4E) and Odonata (Zygoptera). Adults exhibited a more diverse diet (Fig. 4B, C, D, F), including pollinators such as *Apis mellifera*, *Halictus* sp. Latreille, 1804, *Scolia* sp. Fabricius, 1775, *Argynnis paphia* (Linnaeus, 1758), and *Macroglossum stellatarum* (Linnaeus, 1758), but also large or hazardous predators such as wasps (*Polistes* sp., *Vespa crabro* Linnaeus, 1758, *Vespula* sp. Thomson, 1869) or mantises: *Mantis religiosa* (both males and females,

Table 1. Individual survival rate during the 21-day prolificacy test at different population densities (3 sets of boxes with 3, 5, and 10 nymphs each) and with two different feeding regimes (no food or feeding with *Drosophila melanogaster*). The filled-heart symbol (♥) represents a live nymph, the empty-heart symbol (♡) represents a cannibalized nymph, and the cross symbol (+) represents a natural death due to other causes (stress, weakness, disease, etc.).

Day	No food						Food		
	BOX-1 3 nymphs	BOX-2 3 nymphs	BOX-3 5 nymphs	BOX-4 5 nymphs	BOX-5 10 nymphs	BOX-6 10 nymphs	BOX-7 3 nymphs	BOX-8 5 nymphs	BOX-9 10 nymphs
1	♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥
2	♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥
3	♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥
4	♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥
5	♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥++	♥♥♥♥♥♥♥♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♥
6	♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥+++	♥♥♥♥♥♥♥♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♡
7	♥♥♥	♥♥♥	♥♥♥♥♥	♥♥♥♥♥	+++++++	♥♥♥♥♥♥♥+♡♡	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♡
8	♥♥+	♥++	♥♥♥♥♥	♥♥♥♥♥		♥++++♡♡♡♡	♥♥♥	♥♥♥♥♥	♥♥♥♥♥♥♥♥♥♡
9	+++	+++	♥++++	♥♥♥++		♥++++♡♡♡♡	♥♥♡	♥♥♥♥♡	♥♥♥♥♥♥♡♡♡♡
10			+++++	♥♥+++		+++++♡♡♡♡	♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
11				+++++			♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
12							♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
13							♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
14							♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
15							♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
16							♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
17							♥♥♡	♥♥♥♥♡	♥♥♥♥♥♡♡♡♡♡
18							++♡	♥♥♥+♡	♥♥♥♥♥♡♡♡♡♡
19								♥♥♥+♡	♥♥♥+♡♡♡♡♡♡
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21								♥+++♡	♥++♡♡♡♡♡♡

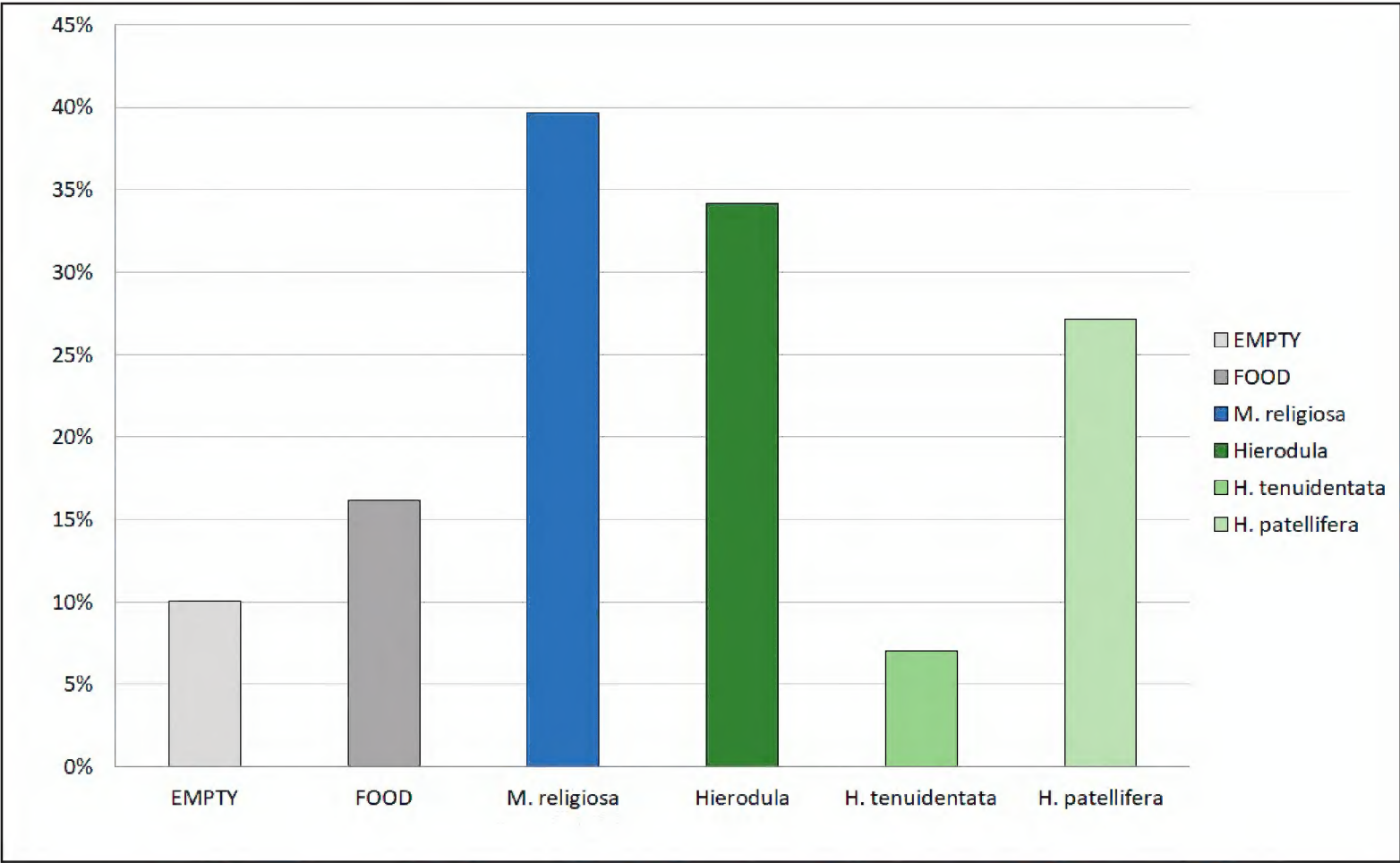


Fig. 3. Time spent (percent outside the central area) by the males of *M. religiosa* in the 4 tubes containing different sources of attraction: empty, food (cockroach), female of *Hierodula* (*tenuidentata* or *patellifera*), and female of *M. religiosa*.

and other *Hierodula* individuals (males and females) (Fig. 8). Even very large or repulsive prey were involved, such as *Anacridium aegyptium* (Linnaeus, 1764), *Halyomorpha halys* (Stål, 1855), and *Nezara viridula* (Linnaeus, 1758).

The four predations on vertebrates (Fig. 5) were recorded on the common wall lizards *Podarcis muralis* (Laurenti 1768) by adult *Hierodula* females and a tree frog *Hyla perrini* Dufresnes et al. (2018) by a *Hierodula* late-instar nymph.

A total of 31 positive interactions with *Hierodula* by other insects (12) (Fig. 6) or vertebrates (19) (Fig. 7) were recorded. They involved 1 Diptera (3%), 8 Hymenoptera (26%), 3 Rhynchota (10%), 14 Mammalia (45%), and 5 Aves (16%). Hornets (*Vespa crabro*) were found to be the major insect predator of *Hierodula*, both for nymphs and adults (males and females). Stink bugs (*Halyomorpha halys* and *Nezara viridula*) were often observed to pierce *Hierodula* oothecae with their rostrum. Ants of the native species *Crematogaster scutellaris* (Olivier, 1792) were observed nesting inside hatched oothecae of *Hierodula*, similar to what has already been observed in the natural Asian range of *Hierodula tenuidentata* (Mirzaee et al. 2021).

Finally, dead *Hierodula* individuals were seen to have been attacked by *Sarcophaga* sp. Meigen, 1826, workers of *Vespula* sp., and *Crematogaster scutellaris*. Vertebrate predators included domestic cats (*Felis catus* Linnaeus, 1758), the Eurasian golden orioles *Oriolus oriolus* (Linnaeus, 1758), and nocturnal raptors (*Athene noctua* (Scopoli, 1769)). Finally, the great spotted woodpeckers *Dendrocopos major* (Linnaeus, 1758) and the blue tits *Cyanistes caeruleus* (Linnaeus, 1758) were observed in the act of detaching, carrying away, and feeding on *Hierodula* oothecae.

Discussion

The evidence collected in the analyses presented here portray the two Asian mantises *H. tenuidentata* and *H. patellifera* as fast-growing, behaviorally flexible alien predators and invasive species, with measurable impacts on Mediterranean and continental European arthropod and vertebrate communities. Their potential for rapid numerical build-up is evident and experimentally supported: In controlled laboratory conditions, an average of 209 first-instar nymphs hatched from *H. tenuidentata* oothecae, roughly twice the productivity documented for the native *Mantis religiosa*, and a very low rate of cannibalism events were seen in the early stages of life of this Asian species. Such high reproductive output suggests a steep intrinsic rate of increase and sets the stage for local numerical dominance within a few reproductive cycles.

Population growth is reinforced by marked reproductive interference. In sex-arena tests, *M. religiosa* males spent 34% of their away-from-center time near tubes containing *Hierodula* females—almost the same amount of time as they were recorded near their conspecific females. When physical barriers were removed, every approaching



Fig. 4. Negative interactions of *Hierodula* preying on invertebrates: A. Muscidae (photo credit: A. Bianchi), B. *Vespa crabro* (photo credit: S. Moro), C. *Argynnis paphia* (photo credit: M. Silenzi), D. *Anacridium aegyptium* (photo credit: D. Maistrello), E. *Cicada orni* (photo credit: S. Tenani), F. *Halyomorpha halys* (photo credit: M. Algeri Bricoli).

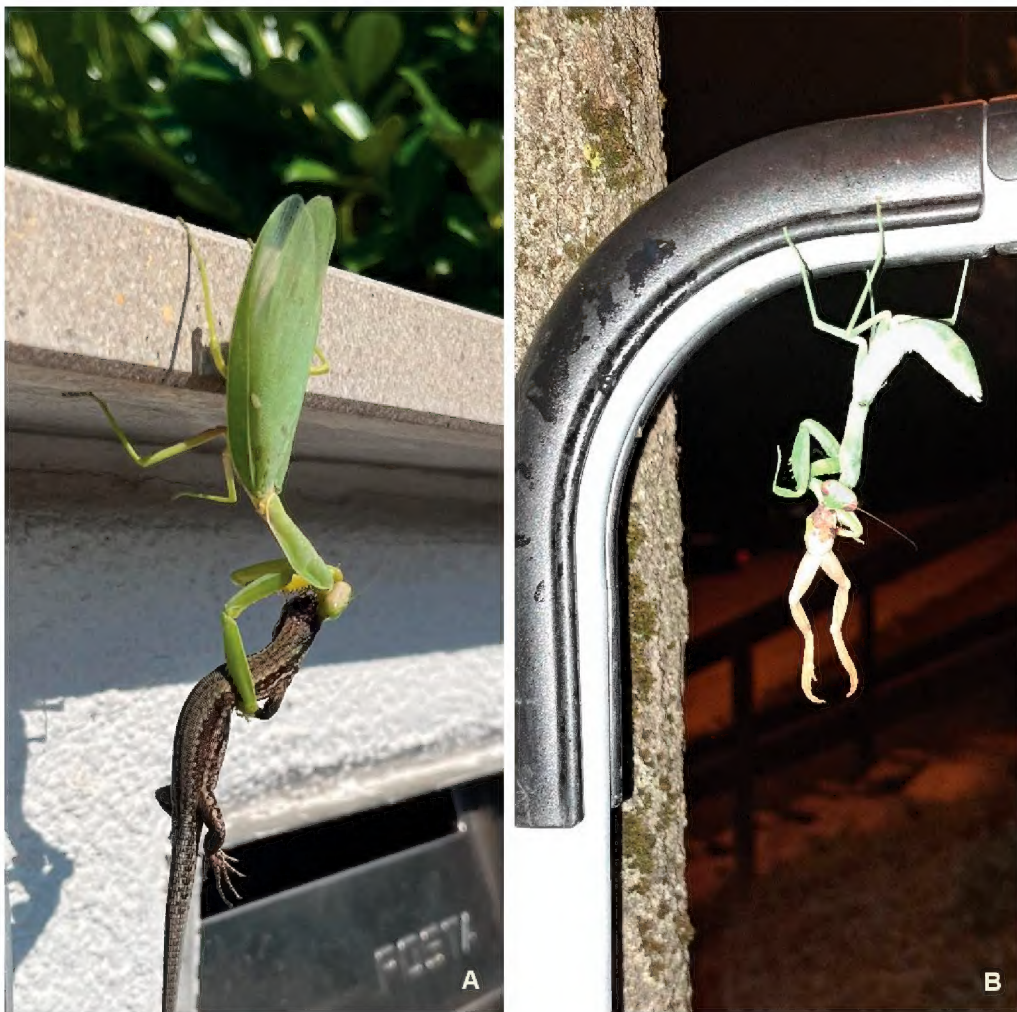


Fig. 5. Negative interactions of *Hierodula* preying on vertebrates. A. *Podarcis muralis* (photo credit: P. Chittaro); B. *Hyla perrini* (photo credit: C. Biscaro).

M. religiosa male was captured and eaten by a *Hierodula* female. This phenomenon closely parallels the “fatal attraction” documented in New Zealand, where males of the endemic *Orthodera novaezealandiae* Colenso 1882 are fatally lured by pheromones of the alien invasive *Miomantis caffra* Saussure 1871 (Fea et al. 2013). Because mate-searching males are the most mobile life-history stage in mantises, even a modest heterospecific misorientation rate may translate into substantial additional mortality, skewing the operational sex ratio of *M. religiosa* and potentially depressing fertilization success in mixed populations. Pheromone-induced interactions need further research at the chemical level since *Hierodula* males seem to have a complex range of responses to female stimuli (Ayano et al. 2025).

Although vertebrate predation events were rare (four cases), all prey taxa (*Podarcis muralis* and *Hyla perrini*) are listed in Annex IV of the EU Habitats Directive (*Hyla perrini* is listed under the old name *Hyla intermedia* Boulenger, 1882). The ability of large *Hierodula* females to subdue amphibians and reptiles underscores a risk of spillover to insular or fragmented habitats harboring micro-endemic herpetofauna (i.e., the recent sighting in August 2024 of *Hierodula* on Elba Island (iNaturalist observation: 239818763) may threaten the local endemic *Podarcis muralis* ssp. *colosii* (Taddei, 1949)), and this awareness may be a priority in other Mediterranean islands with endemic species of vertebrates or invertebrates. This situation needs urgent assessments in the Aegean islands where *Hierodula* has been recorded since 2012 (<https://www.gbif.org/occurrence/3995598619>) and where their populations are still expanding, with unpredictable impacts on delicate island ecosystems.



Fig. 6. Positive interactions of invertebrates preying on *Hierodula*. A. *Vespa crabro* (photo credit: E. Crepet); B. *Crematogaster* sp. (photo credit: A. Previtali); C. *Halyomorpha halys* (photo credit: A. Previtali).



Fig. 7. Positive interactions of vertebrates preying on *Hierodula*. A. *Athene noctua* (photo credit: M. Zambelli); B. *Cyanistes caeruleus* (photo credit: A. Previtali); C. Domestic cat (photo credit: P. Ruggeri); D. *Dendrocopos major* (photo credit: A. Previtali).

Both citizen-science and laboratory observations (Fig. 9) show that *Hierodula* prey mostly on managed pollinators (*Apis mellifera*) and on a suite of wild pollinators (mostly Hymenoptera and Diptera). Simultaneously, they compete with and are frequently preyed on by hornets (*Vespa crabro*), accounting for, together with the domestic cat, the majority of the 31 positive interactions (predation on *Hierodula*). This bidirectional linkage suggests that *Hierodula* could alter local pollination services both directly (consumption of pollinators) and indirectly (affecting hornet–prey dynamics).

No instance of native mantids feeding on *Hierodula* was recorded, and only hornets and vertebrate predators exerted measurable

natural control. The absence of reciprocal predation (Fig. 8) suggests weak top-down resistance within the recipient guild, further facilitating *Hierodula* establishment. The apparent absence of reciprocal predation on *Hierodula* echoes patterns seen with other generalist alien predators, such as the harlequin ladybird *Harmonia axyridis* (Pallas, 1773), whose successful establishment in Europe and North America has been attributed in part to limited natural enemy pressure and strong intraguild predation on native coccinellids (Li et al. 2021). Future studies should consider the role of parasitoids as limiting factors for the expansion of these mantids in Europe. This is not easy to assess with citizen science, but photos have been reported of oothecae damaged or perforated

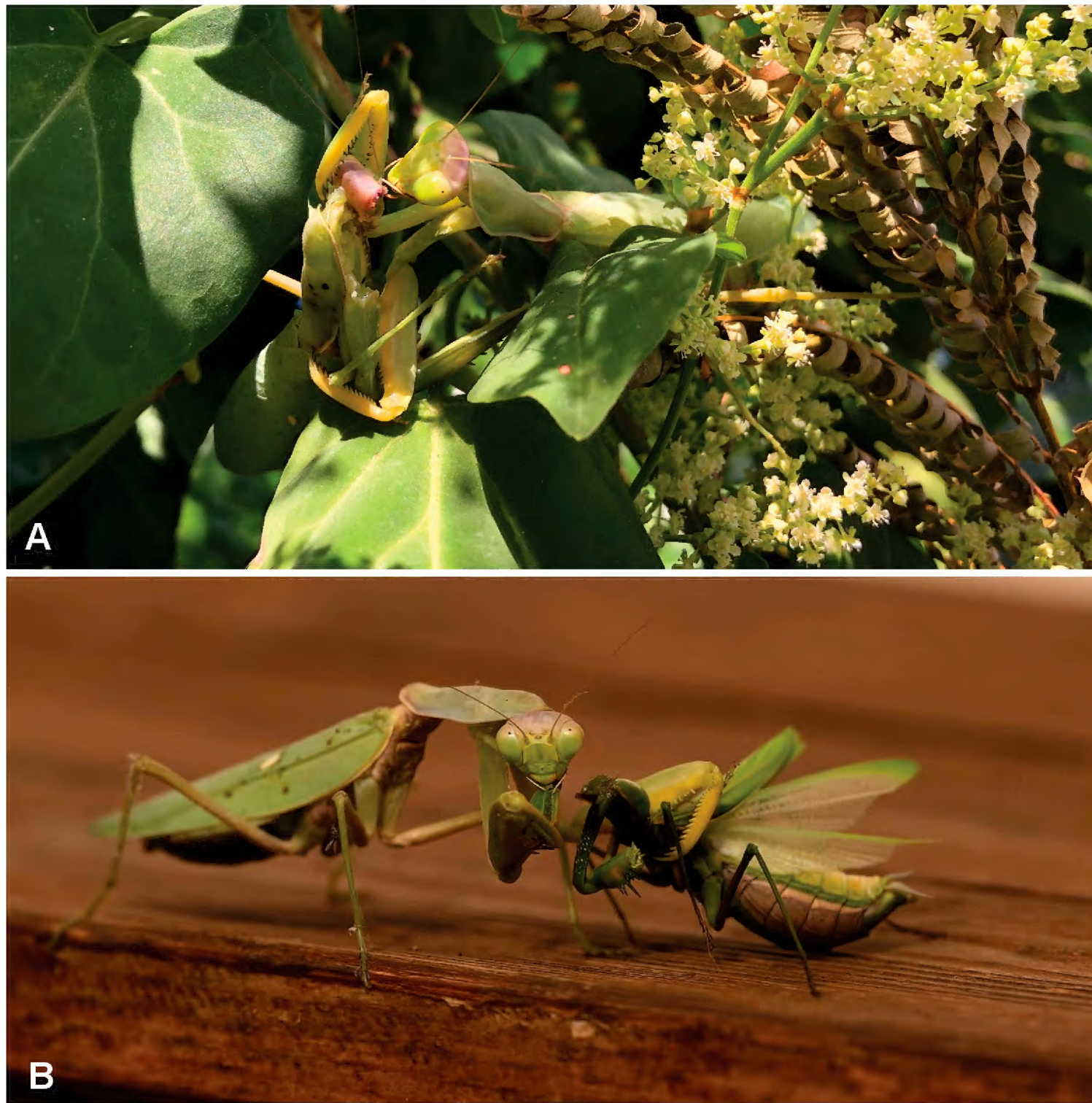


Fig. 8. Interactions between mantises. **A.** *Hierodula* adult female eating another *Hierodula* adult female (photo credit: S. Scornavacchi); **B.** *Hierodula* eating *Mantis religiosa* (photo credit: M. Bonatti).

with holes compatible with those made by the wasp *Podagrion* Spinola 1811, already known to parasitize *Hierodula* egg cases in their area of origin and also present in Europe (Mirzaee et al. 2021), or similar parasitic wasps. Ants, observed here nesting inside the oothecae, are also known to participate in these dynamics (Mirzaee et al. 2021), and a network of new and old competitors and ecological relationships may emerge in the near future.

The trophic generalism documented here, from small dipterans to large cicadas, orthopterans, problematic pentatomid bugs, and challenging vertebrates, implies, as expected, that a generalist predator such as *Hierodula* and, similarly, the African counterpart *Sphodromantis viridis* Forsskal, 1775, which is also spreading fast as an alien species in many Mediterranean islands (Battiston et al. 2017), will exploit whatever prey spectrum is locally abundant. If these mantises can spread into biodiversity hotspots or islands, predation pressure might severely impact endemics or vulnerable species or communities.

Citizen-science data identified the domestic cat as the predominant vertebrate predator of *Hierodula* (45% of positive events). While this may aid in limiting alien mantis numbers, as already reported for other alien species such as grey squirrels (*Sciurus carolinensis* Gmelin, 1788) (Monaco 2014), domestic cats may add further pressure on the already-stressed ecosystems where *Hierodula* is introduced and are clearly not the solution to the problem.

Human habitat modifications can clearly facilitate the spread of *Hierodula*. The presence of this species recorded mostly in urban or sub-urban environments, the use of artificial insect refuges (a *Hierodula* male was here observed while hunting directly over an insect hotel in a garden, similarly to what observed in the USA with *Mantis religiosa* on hummingbird feeders in Nyffeler et al. 2017), and the use of city heat-islands to prolong their life cycle in the colder months of the year (Di Pietro and Battiston 2022) indicate that these mantises are using human activities to spread and survive.

Mantids are mostly sit-and-wait predators that remain hidden and inactive nearly 90% of the time (Prete et al. 1999). Thus, traditional field sampling may underestimate predator-prey events. The over 2,300 georeferenced observations amassed through the “Progetto Mantidi Aliene” platform provided an unprecedented window on rarely witnessed interactions, validating citizen engagement as an indispensable adjunct to conventional monitoring. Citizen science records are usually biased by the attractiveness of the observed event: predations of large mantises on vertebrates are more impressive than predations on smaller common insects and more likely to be recorded and shared, while misidentifications of what are generally considered “common insects” may overlook impacts on rare or endemic invertebrate species. However, these large numbers of records can include an impressive

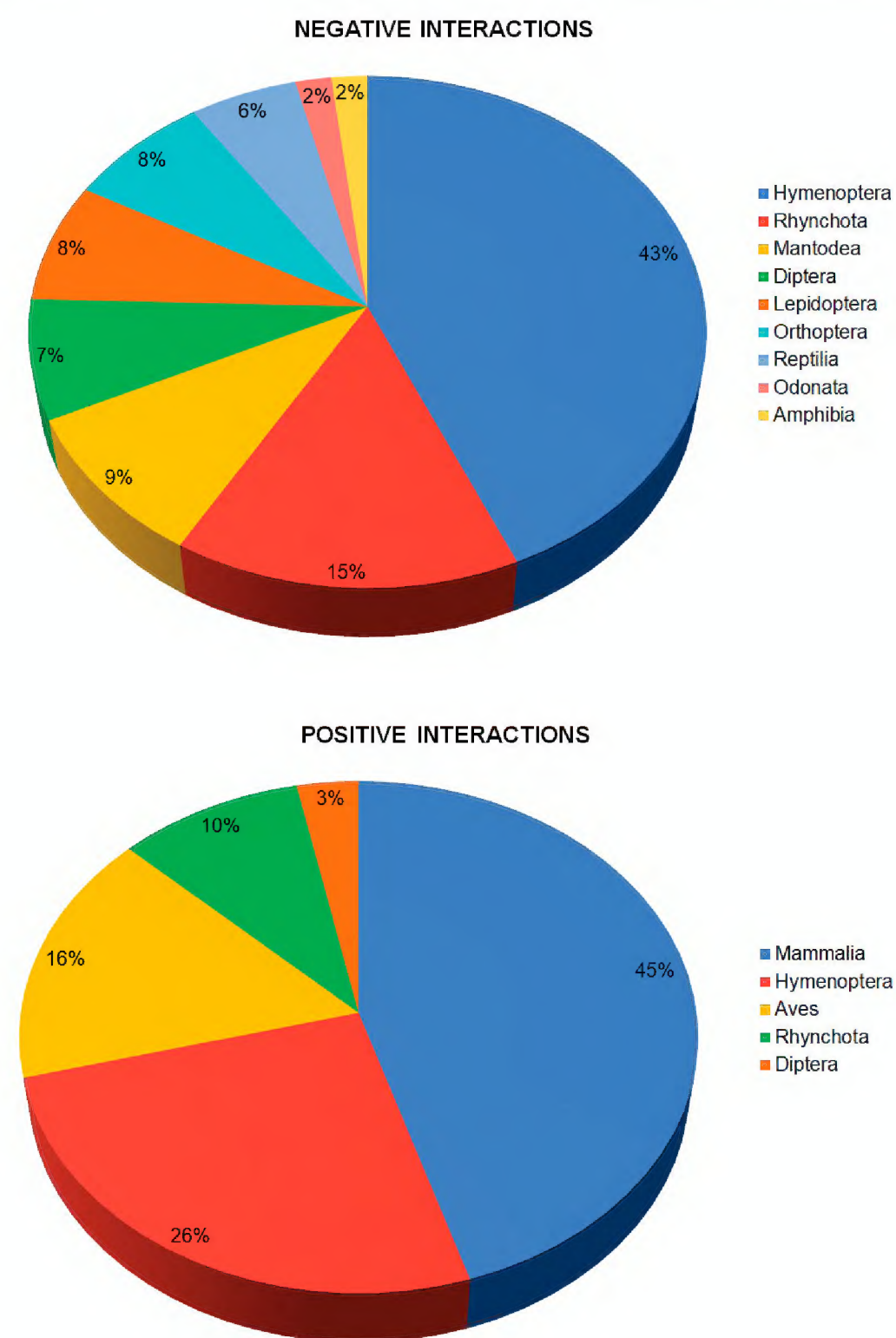


Fig. 9. Overview of the interactions recorded between *Hierodula* and its prey (top) and its predators (down). Percent represents the number of interaction events in the total recorded, grouped by the different orders/classes.

set of anecdotal events to be investigated in further research. This study noted unusual interactions, such as birds feeding on oothecae (something observed also in *Stagmomantis limbata* Hahn 1835 in North America; see Fagan 2002), unexpected negative or even positive interactions between alien species, the transport of ants or arthropod communities inside the oothecae, and necrophagy, opening possibilities for future investigations. In North America, the Chinese mantis *Tenodera sinensis* Saussure, 1871 has repeatedly been shown to depress populations of the smaller native *Stagmomantis carolina* (Johansson, 1763) through both competition and direct predation, with meta-analyses documenting consistent negative effects on multiple arthropod orders and on herbivore guilds overall (Fagan et al. 2002).

It should be noted that competition between different species of mantids was tested here under artificial conditions and that these species already coexist with well-established dynamics in their natural habitats, albeit with different numbers. This coexistence is probably possible because of the separation of niches or microhabitats (i.e., the more pronounced arboreal habitat of *Hierodula* compared to the more grassy habitat of *Mantis*). However, the creation of new dynamics in Europe stems mainly

from urban centers and peri-urban areas where these species coexist in artificial conditions and where niche separation is not always possible. Therefore, the results of this study, with all the limitations of applicability, should still be considered in terms of the development of dynamics between the two species, especially in heavily anthropized territories such as northern Italy or several other European areas. The convergence of traits such as high fecundity, behavioral plasticity, broad diet, and interspecific sexual deception suggests that *Hierodula* could replicate or even exceed these impacts in Europe.

Taken together, the results fulfill key EU and IUCN criteria for biological invasiveness (see IUCN 2020): Exceptionally high reproductive output, demonstrable reproductive interference (competition and predation) with a native mantis species, extensive predation on native vertebrates and pollinators, and exploitation of anthropogenic habitats are 4 of the 12 proposed criteria for invasive species (IUCN 2020) even if the scale of the impacts needs further investigations. Management should, therefore, move beyond simple monitoring to (i) perform detailed risk assessments of *H. tenuidentata* and *H. patellifera* and other alien mantises in Europe (see Schwarz and Ehrmann 2018) using predictive models when monitoring is problematic (Larkin et al. 2025); (ii) apply targeted surveillance in areas hosting endemic or threatened vertebrates, sensitive pollinator or endemic species networks; and (iii) promote public communication discouraging deliberate relocation of individuals or oothecae and encouraging their removal under specialist guidance (as proposed in Battiston et al. 2024). Failure to act promptly could allow these formidable generalists and clearly invasive predators to severely impact European ecosystems.

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